

Changes in gas exchange characteristics during the life span of giant sequoia: implications for response to current and future concentrations of atmospheric ozone

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Summary

Native stands of giant sequoia (*Sequoiadendron giganteum* Bucholz) are being exposed to relatively high concentrations of atmospheric ozone produced in urban and agricultural areas upwind. The expected change in environmental conditions over the next 100 years is likely to be unprecedented in the life span (about 2,500 years) of giant sequoia. We determined changes in physiological responses of three age classes of giant sequoia (current-year, 12-, and 125-year-old) to differing concentrations of ozone, and assessed age-related differences in sensitivity to pollutants by examining physiological changes (gas exchange, water use efficiency) across the life span of giant sequoia (current-year, 2-, 5-, 20-, 125-, and > 2,000-year-old trees). The CO₂ exchange rate (CER) was greater in current-year ($12.1 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) and 2-year-old seedlings ($4.8 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) than in all older trees ($3.0 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, averaged across the four older age classes). Dark respiration was highest for current-year seedlings ($-6.5 \pm 0.7 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) and was increased twofold in symptomatic individuals exposed to elevated ozone concentrations. Stomatal conductance (g_s) was greater in current-year ($355 \text{ mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$) and 2-year-old seedlings ($200 \text{ mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$) than in all older trees ($50 \text{ mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$), indicating that the ozone concentration in substomatal cavities is higher in young seedlings than in trees. Significant changes in water use efficiency, as indicated by C_i/C_a , occurred in trees between ages 5 and 20 years. We conclude that giant sequoias seedlings are sensitive to atmospheric ozone until they are about 5 years old. Low conductance, high water use efficiency, and compact mesophyll all contribute to a natural ozone tolerance, or defense, or both, in foliage of older trees.

Keywords: carbon dioxide exchange, mesophyll, respiration, *Sequoiadendron giganteum*, stomatal conductance, water use efficiency.

Introduction

Widespread increases in atmospheric pollution are predicted not only in urban areas (Kickert and Krupa 1990), but also over forested lands as a result of long distance transport. Pollutants transported east of Los Angeles, California, affect mixed conifer and ponderosa pine forests in the San Bernardino Mountains, where concentrations of atmospheric ozone commonly reach 200 ppb during the summer (Miller et al. 1986). Similarly, pollution produced in the San Francisco Bay area and San Joaquin Valley is transported to Sequoia and Kings Canyon National Parks in the southern Sierra Nevada, California, where concentrations of atmospheric ozone commonly reach 100 ppb during the summer (Grulke et al. 1989). Mature trees of Jeffrey pine

(Peterson et al. 1987) and giant sequoia seedlings (Miller et. al. 1994) show visible ozone damage symptoms.

We investigated the effects of atmospheric ozone on the gas exchange characteristics of current-year seedlings and 12-, and 125-year-old trees by means of a combination of open top chambers (OTCs) and branch exposure chambers (BECs). We also examined the physiological characteristics of current-year and 2-year-old seedlings and 5-, 20-, 125-, and > 2,000-year-old trees growing *in situ* in ambient air in an attempt to explain age-related differences in sensitivity to pollutants. Data for the seedlings and 12-year-old rooted cuttings are summarized from research conducted in open-top chambers (OTCs) in Sequoia National Park (Grulke et al. 1989). Ozone treatments of the three 125-year-old trees were conducted in branch exposure chambers (BECs) located at a height of 35 m within the canopy. The descriptive physiological data were collected from several locations in Sequoia and Kings Canyon National Parks with known fire histories to achieve a uniform population age of current-year and 2-year-old seedlings, and 5-, and 20-year-old trees. Older trees (125-, and > 2,000-year-old) in Giant Forest in Sequoia National Park were sampled at a height of 20 m within the canopy.

Methods

The ozone exposure study sites were located at 1,920 m elevation, in Giant Forest Grove, Sequoia National Park, California. The OTC site was located within a forest stand characterized by giant sequoia, white fir (*Abies concolor* (Gord. and Glend.) Lindl.), and sugar pine (*Pinus lambertiana* Dougl.). For the BEC study, three emergent trees (53 m, 125-years-old) were chosen that could be accessed by a single, 30-m tall scaffold, and were within 100 m of the OTC site. The descriptive studies of the other four age classes (current-year and 2-, 5-, and 20-year-old trees) were conducted *in situ* on sites with known fire history in Sequoia and Kings Canyon National Parks. The 125- and > 2,000-year-old trees used in the descriptive studies were within 0.4 km of the OTC site.

Open top exposure chambers (OTCs)

Current-year seedlings and 12-year-old rooted cuttings were exposed for 24 h daily to charcoal-filtered air (CFA, about 15% ambient ozone concentrations) or elevated ozone (150% ambient concentrations) in four OTCs per treatment from June 4 to September 15, 1988. Ambient ozone averaged 72.1 ± 1.7 ppb (hourly average, 24 h per day); the subambient treatment averaged 13.0 ± 0.3 ppb and the elevated ozone treatment averaged 103.0 ± 1.9 ppb (hourly averages, 24 h per day; actual treatment was 143% of ambient). The OTCs were 2.13 m in diameter, 2.2 m high, and were of standard construction (Heagle et al. 1979). Blower boxes (1.3 hp squirrel cage) provided a chamber exchange rate of two volumes per min. Air entering the chambers was filtered through fiberglass dust and activated charcoal filters. Ozone was generated on demand based on monitored ambient ozone concentrations (see below) and added to the incoming chamber air stream.

Ambient air was sampled continuously upwind from chambers to prevent contamination. Ozone concentrations were determined with an ozone photometer (Dasibi, Model 1000AH), which was calibrated at 2-week intervals. Instantaneous ozone concentration of the ambient air sample was used to control the voltage supplied to the ozone generator (Griffin Technics, Model GTC-0.5b; supplied with dry air: Puregas, Model HF200). Ozone was supplied through 0.25 cm Teflon tubing to a stainless steel manifold, through precision rotometers (Matheson, Model E517A), then out to the elevated ozone treatment chambers. Fine adjustment in ozone distribution to the chambers was achieved by manually adjusting the rotometers. Air was continuously sampled centrally from each chamber with a vacuum pump to a scanning valve (Scanivalve, custom-made), which allowed sequential sampling at 2.5-min intervals on a second ozone monitor.

Data sampling (ozone concentrations, air temperature at seedling level, soil temperature at a depth of 5 cm, and total global radiation (Li-Cor 200SZ)) was controlled by a GW-Basic control program (Hogsett et al. 1985) in conjunction with a data acquisition system (Keithley System 570). Data were automatically stored on a disk and printed after each sampling interval (1 h).

Branch exposure chambers (BECs)

Twelve branches (four each on three trees) in the canopy of 125-year-old trees were exposed for 24 h daily to CFA or elevated ozone (100, 200, or 300% of ambient) from July 23 to September 19, 1990. Ambient ozone averaged 72.8 ± 1.5 ppb (hourly average, 24 h per day); the subambient treatment averaged 13.0 ± 0.3 ppb; the 100% ambient treatment averaged 94.8 ± 2.9 ppb (actual treatment 130% ambient); the 200% ambient treatment averaged 179.5 ± 6.0 ppb (actual treatment 246% ambient), and the 300% ambient treatment averaged 248.4 ± 9.5 ppb (actual treatment 341% ambient). An additional chamberless branch on each tree was also monitored. Approximately 1000 growing points per branch were enclosed within each BEC. All exposures and monitoring were conducted on the SSW aspect of the three trees at a height of 30 m, which corresponded approximately to the upper third of the canopy of these trees as well as associated species in the stand (white fir, sugar pine; oldest giant sequoia emergent to 85 m). The foliage was exposed to full sun for about 5 h daily.

The control program used for air sampling and supply, and ozone monitoring, generation, and delivery to BECs was similar to that used in the OTCs. Signals from both the ambient and chamber air ozone monitors were linked to a data acquisition system (Keithley System 570), and values were processed every 30 min. Air flow to each of the three BECs (1 per tree) was provided by 1/3 hp squirrel blower boxes fitted with a manifold with three butterfly valves to control and equalize air flow to ensure a chamber exchange rate of 2 per min. Air entering the branch chambers was filtered through fiberglass dust and activated charcoal filters. The BEC design was a modification of that described by Teskey et al. (1991), and was 0.7 m in diameter, 1.2 m long, and constructed from aluminum flat bar covered with Teflon film. A

baffle placed 0.3 m from the air intake (0.15 cm) promoted laminar air flow and gas mixing (Houpis et al. 1988).

Sampling for descriptive physiological measurements

For the descriptive physiological measures across the six age classes, gas exchange was measured monthly from June to September 1990 on six plants from each of the current-year and 2-, 5-, and 20-year-old trees growing in microsites with 2 h of full sun daily. Seasonal maxima for trees in the younger age classes (≤ 20 -year-old) occurred when soil water was depleted. Three trees each from the ≥ 125 - and the $> 2,000$ -year age range were sampled monthly to determine seasonal maxima. The same three trees and an additional three trees per age class were sampled on June 16 and 17 (≥ 125 -year age range) and June 10 and 11 ($> 2,000$ -year age range) to obtain a measure of population variability. All trees for the two older age classes were measured at a canopy height of 20 m by means of a truck equipped with a lift bucket.

Gas exchange measures

Both CER and g_s were measured with an LI 6200 photosynthetic system (Li-Cor Inc., Lincoln, NE) on current-year foliage at $1200 \mu\text{mol m}^{-2} \text{s}^{-1}$. Measures of CER were matched with respiration measured after 15 min of dark adaptation, which was experimentally determined to be the appropriate length of time to exclude photorespiration for giant sequoia. Seedlings from the OTCs were measured in a custom-made cuvette (75.6 cm^3 ; Grulke et al. 1989). Foliage from all other trees was measured in a 250-cm^3 Li-Cor cuvette. Plants in the OTCs were removed for measurement, and plants in the BECs were measured through an opening in the BECs. Means and standard errors were obtained from 2–4 runs (3–4 observations of gas exchange averaged together per run) on each plant over 1–5 min. Leaf temperatures of seedlings and 12-year-old rooted cuttings during gas exchange measurements were within $\pm 1^\circ \text{C}$ of each other.

In the OTC experiment, two seedlings from each of the four chambers of each treatment (charcoal-filtered air and 150% ambient ozone) were sampled for gas exchange. Few rooted cuttings survived in the OTCs because of poor root development, so a total of five cuttings each from the CFA OTCs and elevated ozone OTCs were pooled (i.e., no chamber replicates). All plants in the OTC experiment were measured between September 1 and 5, 1988, and were well watered the evening before and the morning of the gas exchange measurements.

Leaf area determinations

Leaf area of each current-year seedling in the OTCs was determined by a photograph taken from directly overhead with a millimeter rule included for scale. Leaf surface area that intercepted light directly (overlapping needle surface area excluded) was determined by cutting out and weighing the image.

Leaf surface areas of the rooted cuttings in the OTCs, the branchlets sampled in the BECs, and for age classes 2- to $> 2,000$ -year-old trees in the descriptive study

were determined by developing a regression between branchlet surface area and branchlet length for each age class. Needles on branchlets in these age classes are approximately cone-shaped with photosynthetic tissue appressed to the twig. To determine surface area for the regression, height and diameter of each needle on a branchlet were measured and applied in the equation of the surface area of a cone. The surface area of the twig was calculated from length and diameter measures in a cylindrical model, then added to that of the needles. Twenty to thirty branchlets of varying lengths were used to develop the regression between branchlet surface area and length within a tree age class. Correlation coefficients for the regression equations ranged between 0.97 and 0.99.

Needles on current-year seedlings were essentially long, flat, triangles with both surfaces photosynthetically active. Needles were attached to cylindrical, photosynthetic stems. Because specific leaf area varied greatly between sampling periods and seedlings, surface area was determined independently for each seedling. Because of the difference in deducing leaf area of trees in the OTCs and of trees used in the descriptive studies, and because the seedlings in the OTCs were watered twice weekly, the gas exchange measurements of these two aspects of the study are not directly comparable.

Results

Foliage response to elevated ozone concentrations

Seedlings exposed to elevated ozone concentrations in OTCs had visible symptoms of injury, including chlorotic mottling and necrotic needle tips, whereas seedlings grown in CFA were asymptomatic. The CER was significantly lower (5.4 ± 0.6 versus $3.0 \pm 0.4 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$; $P = 0.001$; t -test) and dark respiration was significantly higher (-2.5 ± 0.4 versus $-5.3 \pm 0.7 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$; $P = 0.001$; t -test) in seedlings in the elevated ozone treatment than in seedlings in the charcoal-filtered air treatment (Table 1; summarized from Grulke et al. 1989). Rooted 12-year-old cuttings had lower CER in the elevated ozone treatment (all were asymptomatic) than in the CFA treatment, but differences were not significant (Table 1; summarized from Grulke et al. 1989).

Although differences between treatments were not significant (one-way ANOVA; Table 1), CER of current-year foliage in the BECs decreased with increasing exposure to ozone from 15 to 200% ambient ozone (15% ambient, 2.6 ± 0.4 ; 100% ambient, 2.4 ± 0.3 ; and 200% ambient, $2.0 \pm 0.0 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$). Exposure to 300% ambient ozone did not further decrease CER ($2.1 \pm 0.1 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$). There were no statistically significant differences in dark-adapted respiration across ozone treatments (Table 1).

Gas exchange characteristics across age classes

Mean CERs for sunny microsites over the growing season of plants within an age class were used to demonstrate changes in gas exchange characteristics across each

Table 1. Means \pm one standard error of CER ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) in CFA and elevated atmospheric ozone OTCs for seedlings and rooted cuttings in 1988 and in BECs for foliage on 125-year-old giant sequoia trees in 1990. Cumulative ozone exposure is given at the time of physiological measurements. Similar letters denote no significant difference at the probability given. For two-measure comparisons, a Fisher *t*-test was used, and a one-way ANOVA was used for multiple comparisons.

Ozone concentration (% of ambient)	Chamber type	Cumulative [O ₃] (ppm-h)	CER of current-year foliage			Dark-adapted respiration	
			Seedlings (<i>P</i> = 0.001)	12-Year rooted cuttings (<i>P</i> > 0.05)	125-Year-old trees (<i>P</i> > 0.05)	Seedlings (<i>P</i> = 0.001)	125-Year-old trees (<i>P</i> > 0.05)
15	OTC	21	5.42 \pm 0.60 a	3.34 \pm 1.60 a	—	−2.55 \pm 0.36 a	—
150	OTC	209	3.03 \pm 0.38 b	2.47 \pm 0.70 a	—	−5.29 \pm 0.66 b	—
15	BEC	19	—	—	2.63 \pm 0.39 a	—	−0.85 \pm 0.21 a
100	BEC	128	—	—	2.40 \pm 0.32 a	—	−0.98 \pm 0.03 a
200	BEC	240	—	—	1.96 \pm 0.02 a	—	−1.06 \pm 0.14 a
300	BEC	331	—	—	2.12 \pm 0.11 a	—	−1.06 \pm 0.20 a

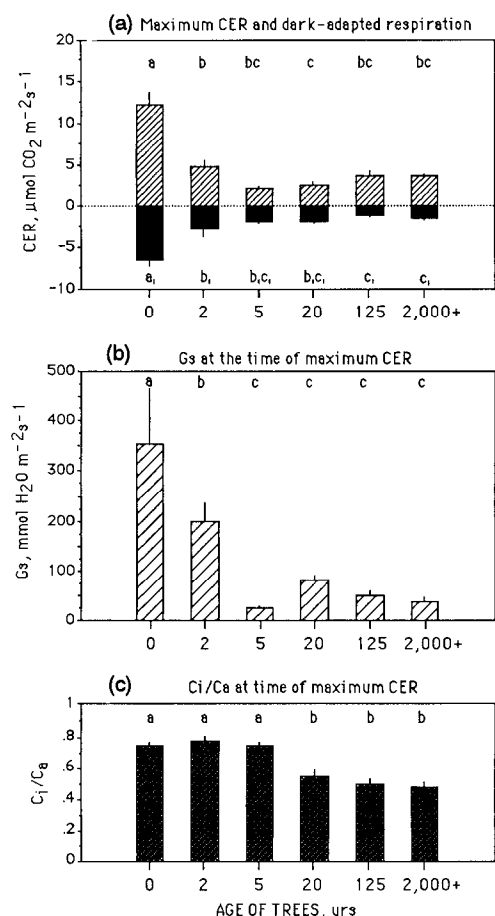


Figure 1. Gas exchange characteristics for six ages of giant sequoia at the seasonal maximum of CER; (a) Maximum CER and dark-adapted respiration; (b) g_s at the time of maximum CER; (c) C_i/C_a at the time of maximum CER. Bar heights denote means \pm one standard error for $n = 6$. Similar letters denote no significant difference at $P = 0.05$, based on a Fisher t -test between any two measures.

of the six age classes (Figure 1). Additional gas exchange characteristics (respiration, g_s , C_i/C_a) are given for the same time as the CER maxima. For the current-year and 2-, 5-, and 20-year age classes, the seasonal maxima occurred between June 27 and July 2 (± 6 days; $P > 0.05$). For the three trees in the 125-year age class sampled throughout the growing season, two trees had a seasonal maximum CER on June 2 and one tree had a maximum CER on August 13. All of the trees in the $> 2,000$ -year age class had a maximum CER on June 3.

Maximum CER was significantly more in current-year seedlings than in 2-year-old seedlings (12.1 ± 1.5 versus $4.8 \pm 0.7 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, $P < 0.05$), and significantly more in 2- than 5-year-old seedlings (4.8 ± 0.7 versus $2.8 \pm 0.2 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, $P < 0.05$). There was no significant difference in seasonal maximum CER in trees older than 5 years.

Rates of dark-adapted respiration were significantly higher for current-year seedlings than for 2-year-old trees (-6.5 ± 0.7 versus $-2.8 \pm 0.8 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$, $P < 0.05$) (Figure 1a). Respiration was not corrected for differences in leaf temperature at the time of measurement. Leaf temperatures of seedlings growing close to the forest floor were $36\text{--}38^\circ\text{C}$ ($4\text{--}6^\circ\text{C}$ greater on average than those for the 2-year-old trees). Rates of dark-adapted respiration did not differ significantly among the 2-, 5-, and 20-year-old trees. Dark respiration rates of the ≥ 125 - ($-1.1 \pm 0.2 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) and $> 2,000$ -year age classes ($-1.3 \pm 0.4 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) were significantly lower than those of the 2-year-old trees ($-2.8 \pm 0.8 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) ($P < 0.05$).

Stomatal conductance (g_s) was variable in current-year seedlings (Figure 1b), but significantly greater than in 2-year-old trees (355 ± 116 versus $200 \pm 36 \mu\text{mol H}_2\text{O m}^{-2} \text{ s}^{-1}$, $P < 0.05$). Current-year and 2-year-old trees had significantly greater g_s than older trees ($P = 0.001$). As inferred from C_i/C_a values, there were significant increases in water use efficiency with tree age (0.48 ± 0.04 to 0.75 ± 0.04 for 20-, 125- and $> 2,000$ -year-old trees, respectively, versus 0.75 ± 0.02 to 0.78 ± 0.01 for current-year, 2- and 5-year-old trees, respectively) ($P = 0.001$; Figure 1c).

Discussion

Elevated ozone concentrations resulted in significantly reduced CER for foliage of current-year seedlings, but not for foliage of 12-year-old rooted cuttings or branches on 125-year-old trees. High stomatal conductance of seedlings facilitated greater ozone transfer to substomatal cavities, and greater intracellular ozone concentrations, as well as increased respiration caused by the by-products of ozone detoxification mechanisms within the leaf (Bytnerowicz and Grulke 1992). Because water use efficiency is lower in seedlings than in older trees, they receive a greater ozone dose per unit of photosynthate accumulated. In giant sequoia, leaf mesophyll becomes increasingly compact with tree age (Miller et al. 1994), and ozone may decompose within the substomatal cavity in foliage on older trees before it reaches the cell. Based on the CER, respiration, g_s , and water use efficiency measurements, we conclude that giant sequoia seedlings are particularly sensitive to atmospheric ozone until they are about 5 years old.

Only one other study has tested the responses to ozone exposure of foliage on different aged trees (Samuelson and Edwards 1993). In their study on red oak, elevated ozone (up to 87 ppm-h) had no effect on the gas exchange characteristics of 2-year-old seedlings or the upper canopy of 30-year-old trees. However, there were deleterious effects on gas exchange characteristics at ozone concentrations of 51 ppm-h in the shaded, lower canopy of the 30-year-old trees. At mid-canopy, elevated ozone reduced leaf biomass by decreasing leaf area.

In the present study, seedlings and rooted cuttings of 12-year-old trees were exposed to full sun for 2 h daily, and branches on the 125-year-old trees were exposed to 4–5 h full sun daily. Light compensation point in elevated ozone was twice that in charcoal-filtered air (95 ± 15 versus $60 \pm 10 \mu\text{mol m}^{-2} \text{ s}^{-1}$) and CER at light saturation was significantly lower in the elevated ozone treatment (5.4 ± 0.6 versus

$3.0 \pm 0.4 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$; Grulke et al. 1989). We conclude that, with increasing ozone concentrations, the radiation interception per unit leaf area necessary to maintain a positive carbon balance in *Sequoiadendron giganteum* will also increase, which is consistent with the finding that elevated ozone reduced whole seedling and root biomass of giant sequoia when plants received less than 2 h of full sun daily (Miller et al. 1994). If light regime is an overriding factor in determining sensitivity to atmospheric ozone within a tree age class, seedling analogs may aid in predicting whole canopy responses.

All gas exchange measures of the six age classes of giant sequoia were made *in situ* in ambient ozone. In ozone-free air, there might be greater differences in net carbon balance of foliage on different ages of trees, because CER of young trees is more depressed by ozone exposure than that of older trees. In younger trees, other environmental factors (drought, limiting light) may combine with ozone to cause mortality. Low conductance, high water use efficiency, and compact mesophyll all contributed to a natural ozone tolerance in foliage of the older trees. The expected increase in atmospheric CO_2 concentrations on g_s enhance ozone tolerance by reducing stomatal conductance.

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